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The effect of acoustic shielding of the region of a dolphin's mental foramina on its hearing sensitivity

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Abstract

The effect of acoustic shielding of the mental foramina of a bottlenose dolphin (*Tursiops truncatus*) on its auditory thresholds has been experimentally studied using the method of instrumental conditioned reflexes with food reinforcement. The detection thresholds of short broadband acoustic pulses deteriorated significantly (by 30–50 dB) under conditions of acoustic shielding in the region of the mental foramina over the whole frequency band of the dolphin's hearing. Therefore, the mental foramina of its lower jaw take part in receiving and conducting the sounds into the mandibular fat in the entire frequency range of the dolphin's hearing. The obtained results give an experimental proof for the assumption that the morphological structures of the lower jaw play a role of the peripheral part of a dolphin's hearing. Now there are grounds to assume that Odontoceti have the similar peripheral part of their hearing. This assumption is based on the similarity of their morphology.

Keywords: Dolphin; Hearing threshold; Mental foramina; Shielding; Acoustics; Lower jaw.

Introduction

The sound conduction mechanisms in the middle ear of toothed whales have been studied in numerous papers. Several researchers of this problem believe that sound travels to the cochlea through the external auditory canal and the middle ear; another viewpoint is that the ear canals cannot at all participate in conducting sound to the middle ear [1] or serve for carrying signals with frequencies below 30 kHz [2]. Other studies suggest that sound can be directly transmitted through the mandibular fat to the tympanic bone, bypassing the external auditory canals and the tympanic ligament [1–4].

Norris suggested [3] that sound can be transmitted to the mandibular fat through the mental foramina. Although this author later advanced another hypothesis about the pathway of sound transmission into the mandibular fat, directly through the posterolateral wall of the mandibular bone, in a specific place he called 'an acoustic window' [4]. Sound is transmitted through the mandibular fat to the lateral wall of the tympanic bone, where its thickness is minimal, and the wall acts as an eardrum, transmitting sound waves to the malleus of the middle ear [3–6]. It was also established that acoustic stimulation of the mandible excites significant evoked potentials in the central auditory system of the dolphin [1,4]. However, Refs.

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[1,4,7,8] disagreed on the location of the area of maximum sensitivity to the sounds emitted by a point source on the surface of the mandible, and the findings do not explain the mechanism of sound conduction.

There is also a number of studies in which the authors claim that toothed whales receive echo signals by their teeth [9]. In these studies, each tooth is regarded as a passive resonator excited by the reflected echo signal and tooth nerves as acoustic pressure transducers. Each row of teeth is considered to be an equidistant antenna array consisting of receivers with a narrow directivity, whose signals are transmitted via the tooth nerves directly into the central nervous system (bypassing the cochlea).

The results of the studies on the subject are thus rather ambiguous and contradictory, and the main question about the mechanisms of sound reception and conduction to the middle ear of toothed whales is currently unanswered. However, the findings of Refs. [10,12,13] suggest that sound travels to the mandibular fat of the dolphin through the mental foramina (MF) of the mandible.

The results of studying the morphology of the dolphin's mandible and the subsequent modeling of the mechanisms of sound reception and conduction through the mandibular canals to the middle ear confirm this assumption. Moreover, in terms of acoustics and the theory of group antennas, each row of the MF acts as an acoustic antenna of the traveling wave, located in the throat of an acoustic catenoidal horn (whose role is played by the corresponding mandibular canal). The concept of the mandible as a system of two traveling wave antennas explains the mechanisms of reception and conduction of sound to the middle ear. In view of this, the morphological structures of each of the halves of the lower jaw (mental foramina, mandibular canal and mandibular fat) are treated as the components of the hypothetical peripheral division of the dolphin's hearing.

The purpose of this study is to experimentally explore the role of mental foramina in the dolphin's hearing. The specific tasks consisted of determining the effect of acoustic shielding of mental foramina on the auditory thresholds of detecting acoustic pulses with peak energies at different frequencies.

The subject of the study, materials and experimental procedures

The experiments were carried out at the T.I. Vyazemsky Karadag scientific station – Nature Reserve of RAS (Feodosia) in an enclosed concrete

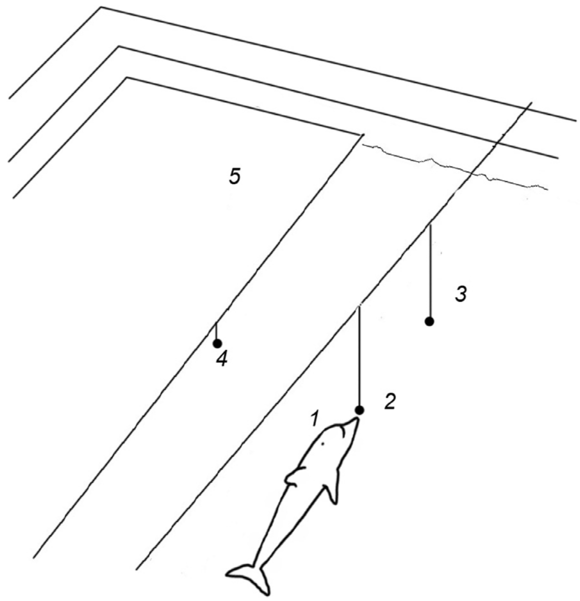

Fig. 1. Experimental setup: dolphin *1* in the starting position, start arm *2*, transducer of acoustic stimuli *3*, signal arm *4*, experimenter's walkway *5*.

27 m × 9 m × 4.5 m-sized pool. An adult Black Sea bottlenose dolphin (*Tursiops truncatus*) who had not previously participated in acoustic experiments acted as the experimental subject. We employed the technique of instrumental conditioned reflexes with food reinforcement using the 'go/no-go' paradigm [14].

On a signal from the trainer (position *5* in Fig. 1), the dolphin was trained to swim to the walkway, where the trainer placed (or did not place) a sound-shielding hood on the rostrum of the animal in the MF area. After that, the dolphin was signaled to swim to start arm *2* suspended at a depth of 1 m, and remained at that depth with almost no movement (quasi-stationary), touching the tip of the start arm with its rostrum. After a few seconds the experimenter turned on the auditory stimulus (shown in Fig. 2) that the dolphin found (or did not). If the stimulus was produced and the dolphin found it, the dolphin left the starting position (go) and pressed its rostrum against signal arm *4* (located near the surface of the water), thus indicating that it had found the stimulus. If the stimulus was not presented, the dolphin remained at the starting position until receiving a signal from the trainer (no-go). In these cases, the dolphin received food reinforcement for correctly solving the problem. If necessary, the trainer removed the shielding hood from the dolphin's rostrum for that purpose every time. The cases when a stimulus was produced but the dolphin did not approach the signal arm, or there was no

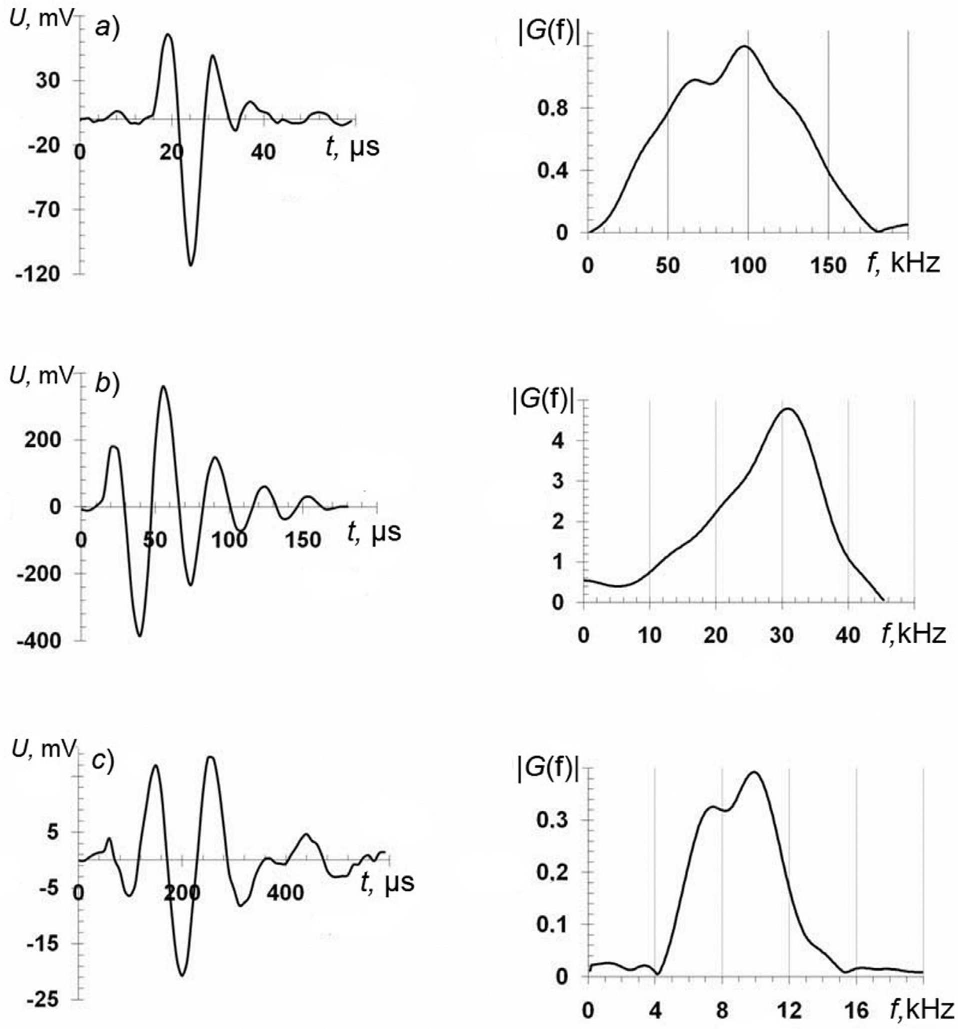

Fig. 2. Examples of waveforms $U(t)$ and the corresponding frequency spectra $|G(f)|$ of acoustic pulse signals with the maxima at frequencies around 100 kHz (*a*), 30 kHz (*b*) and 8 kHz (*c*). Signals were used as acoustic stimuli.

stimulus but the dolphin approached the signal arm (a false alarm) were regarded as errors and were not rewarded.

In each test, the order of the positive and negative stimuli (i.e., the stimuli were either produced or not) was random (but no more than three identical stimuli could be produced in a row).

Each threshold value of the sound pressure level (SPL) of the stimulus was determined by at least three sessions. Each session consisted of about 60 tests. Typically, the stimuli with the SPL significantly exceeding the threshold were produced in the first tests of each session. Throughout the session, the SPL of the stimuli gradually decreased (with a step of 3 dB) to the threshold values (50% of the level of correct responses). The SPL of a stimulus then increased by 4–6 dB, up to the correct reactions of the animal, and the threshold (a decrease in the SPL of the stimulus) was again approached with a step of 3 dB steps. The threshold SPL value of the stimuli corresponding to 75% of correct answers was calculated by averaging between the maximum subthreshold and the minimum superthreshold values of their SPL. The latter were obtained by repeatedly crossing the threshold.

To reduce the effect of interference of the direct signal and of those reflected by the pool on the results of the experiments, short broadband acoustic pulse signals from a special transmitter (position *3* in Fig. 1) located at a distance of 2 m from the start arm, and at a depth of 1 m were used as stimuli. The distance between transducer *3* and the wall of the pool was 3 m.

Stimuli with the energy peaks at frequencies of 30, 60 and 100 kHz were formed through a reaction of spherical acoustic transducers made of piezoelectric ceramics, 50, 30 and 20 mm in diameter, to rectangular pulses of 17, 9 and 5 μs, respectively. A transducer with a diameter of 50 mm was used for obtaining pulses with energy peaks at frequencies of 8 or 16 kHz. The transducer was excited by a rectangular pulse with the duration of 56 or 36 microseconds through an octave band filter with the central frequency of 8 or 16 kHz, respectively. Examples of the stimuli applied are shown in Fig. 2. The waveforms were detected with the emitter and the receiver submerged to a depth of 1 m, at a distance of 1 m away from each other. The amplitude of the rectangular pulse exciting the emitter was 20 V. A calibrated 8103 hydrophone with a precision 2650 amplifier (40 dB gain) by the B&K company was used as a receiver. The duration of the stimuli did not exceed three periods of the corresponding frequency of the peak acoustic pulse energy. In this case, the reflections of the stimulus from the pool walls and the water surface did not overlap with the direct stimulus, as they arrived with a sufficient time delay and were significantly attenuated compared to it. For the threshold SPL values of the stimulus, the reflection levels were below the auditory pulse detection threshold of the dolphins, which allowed to perform measurements without special sound-absorbing coatings.

The acoustically opaque hood for the MF (Fig. 3) was made in the shape of the dolphin's rostrum and was snugly fit over it. The length of the hood was about 15 cm. It was made from a 5 mm-thick sheet of neoprene foam with closed pores. This material has a high strength and high water and oil resistance. Due to these properties it can retain its sound-shielding properties provided by gas bubbles within its pores for a long time. The efficiency of this sound-shielding material was measured prior to the experiments. The attenuation of the peak sound pressure for wideband short pulses with energy maxima at frequencies of 10, 55 and 170 kHz as the pulses were shielded by one layer of this material for normally incident sound reached 28, 32 and 36 dB, respectively.

We should note that the wavelengths corresponding to the frequencies of the energy peaks of the stimuli used in the experiment lie in the range from 1.5 to 20 cm, so the linear dimensions of the shield at low acoustic frequencies become smaller than the stimuli wavelengths. Because of this, in order to improve the shielding efficiency, the hood had the appropriate shape, covering both the upper and the lower jaws (see Fig. 3). If the hood were made to match only the shape of the outer surface shape of the lower jaw, the effectiveness of such a shield would be lower even at a frequency of 100 kHz (1.5 cm wavelength) due to diffraction. Shielding by such a device would not occur at all at frequencies well below 8 kHz (wavelength of more than 19 cm), since the distance from the edge of the hood to the MF would be less than 2 cm.

Experimental results

In this paper, we measured the auditory thresholds at which the dolphin can detect short broadband acoustic pulses with energy peaks at frequencies of 8, 16, 30, 60 and 100 kHz, as well as the detection thresholds for the same pulses under acoustic shielding of the MF. The measurement results (Fig. 4) are represented as a function showing the relative deterioration of the auditory thresholds for detecting the stimuli, caused by the acoustic shielding of the MF. Taking into account that the stimuli were broadband (see Fig. 2), shielding efficiency was high over the entire frequency range examined (6–160 kHz), and increased with frequency from 30 to 50 dB.

For better clarity of the results obtained, the same figure shows the calculated dependence of sound wavelength in water versus frequency. It is noteworthy that the dependence of MF shielding efficiency versus frequency is the mirror image of the frequency dependence of the sound wavelength in water. This result indicates that the shielding efficiency is inversely proportional to the wavelength and hence is determined by the wavelength of sound.

The measurement results for the absolute values of the stimuli detection thresholds in this experiment are consistent with the audiogram of the bottlenose dolphin [15] taking into account the phenomenon of energy summation [16–18]. This further proves that the dolphin studied in our experiment had normal hearing.

The specifics of the dolphin's mandibular foramina, namely their dimensions, shape and architecture are governed by acoustic feasibility [10,12,13]. This natural conclusion, based on the results of the morphological study and the results of modeling the mechanisms of sound reception and conduction through the mental foramina to the middle ear of the dolphin, is confirmed to a large extent by the experimental results obtained (see Fig. 4). Under MF shielding, the

Fig. 3. Photograph of the dolphin with an acoustically opaque hood covering the area of its mandibular foramina; made near the walkway.

mean values of the auditory thresholds for detecting pulses with energy peaks at frequencies of 8, 16, 30, 60 and 100 kHz grow by 30, 34, 40, 46 and 50 dB, respectively. This means that such shielding significantly impairs the sensitivity of the dolphin's hearing in the 6–160 kHz frequency range (taking into to account that the stimuli are broadband), i.e., over the whole frequency band of the dolphin's hearing. Therefore, the mental foramina are involved in receiving and conducting sounds to the mandibular fat, and are the only sound-conducting channel for the sounds of all frequencies used in the experiment.

At the same time, a decrease in the MF shielding efficiency with a decrease in stimuli frequency reaching 20 dB can be attributed to the increasing penetration of sound into the hood with an increase in the stimuli wavelength as a result of diffraction. The sound wavelength increases significantly with a decrease in frequency (see curve *2* in Fig. 4). Moreover, while the dimensions of the acoustic shielding at frequencies of about 100 kHz exceed the wavelength of the stimulus sound by 10 times, the linear dimensions of the shield become comparable to the wavelength at frequencies around 16 kHz, and are even smaller than the wavelength of sound at a frequency of about 8 kHz. It follows from the theory and the results obtained that shielding efficiency is the highest at a maximum ratio of the shield dimensions to the wavelength (the value

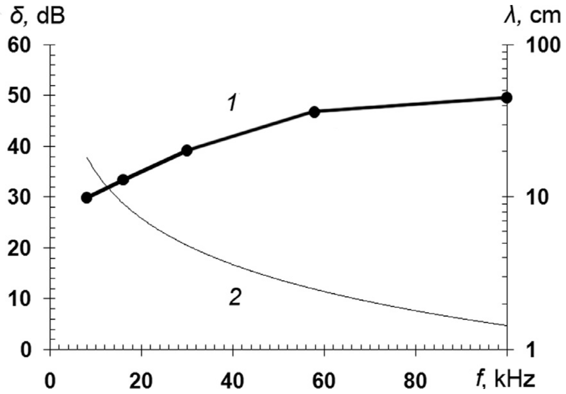

Fig. 4. Frequency dependences for the attenuation range of the dolphin's auditory thresholds with the special hood used (*1*) and for the wavelength of sound in water (*2*). The quantity δ is the ratio of the mean auditory threshold for the dolphin detecting acoustic pulses under MF shielding to the corresponding value without shielding; f is the peak energy frequency of the acoustic pulses $|G(f)|$ and the frequency of sound in water.

at 100 kHz in Fig. 4). Additionally, for a hood with these dimensions, the sound-shielding efficiency becomes even higher than the shielding efficiency of the material from which the hood is made. This is due to the fact that sounds are transmitted the mandible (and hence to the hood) almost tangentially and travel a path in the material that is substantially longer than its thickness.

If we take into account the effect of diffraction, it becomes clear that the efficiency of MF shielding at the measured frequencies would have been the same at a constant ratio of the screen size to the wavelength. This is also attested by the fact that the threshold values change inversely proportional to the wavelength (see Fig. 4). Unfortunately, at low frequencies, it is difficult to provide the same ratio between the shield dimensions and the stimuli wavelength as for the frequency of 100 kHz, as the shield dimensions would be too large in this case (for example, 1.9 m for a frequency of 8 kHz), and because of this, the efficiency of the hood used decreases with the decreasing frequency.

The original results obtained in this study indicate that the MF are involved in receiving and conducting sounds to the mandibular fat and further to the tympanic wall, i.e., to the middle ear, providing a unique sound-conducting channel. This fact excludes the possibility of sound conduction through other channels [4,7,8,19–23].

MF shielding efficiency at frequencies below 6 kHz was not measured in the present study, but we can assume that sound is received and conducted by the same unique channel, i.e., through the MF, at low frequencies as well. This is supported by the constant slope (9–10 dB/octave) of the low-frequency branch of the dolphin's audiogram [15], which starts at about 0.1 kHz and extends up to 20–30 kHz.

Conclusion

This paper examined the effect of acoustic shielding of the dolphin's mental foramina on the auditory thresholds for detecting acoustic pulses with energy peaks at different frequencies.

The results of measuring these auditory thresholds with the mental foramina area shielded and unshielded provide further experimental confirmation for the hypothesis advanced concerning the decisive role of the morphological structures of the dolphin's mandible as a new peripheral region of its auditory system [11–13,24–26]. This hypothesis was based on the results of a morphological study and of modeling the system under consideration.

Thus, mental foramina act as the new outer ear canals. They are involved in receiving and conducting sounds to the mandibular fat in the whole frequency range of the dolphin's hearing (0.1–160 kHz). The mandibular fat transmits the sounds to the lateral wall of the tympanic bone, i.e., to the middle ear and the cochlea, which is consistent with Refs. [3–6]. The results of this study give reason to assume that the toothed whales (Odontoceti) possess this new peripheral hearing region due to the similarity of their morphology.

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